

Avian diversity in a Kenyan agroecosystem: effects of habitat structure and proximity to forest

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Abstract Tropical agroecosystems cover an increasingly large proportion of the Earth's terrestrial surface. Yet, relatively little is known about the factors that influence their avifauna, especially in areas of high human population density. The potential of tropical farmland for sustaining bird biodiversity, including forest birds, can be influenced by habitat structure and the distance from the nearest forest. We investigated the effect of these two factors on the bird community in the farmland near Kakamega Forest, Kenya. Using point counts, we assessed the number of bird species and individuals on 56 study plots in distances up to about 2,100 m from the forest. We observed a total of 96 bird species in the farmland, 22 of which were forest, 58 shrub-land, and 16 open-country species. High vertical vegetation heterogeneity and a large number of woody plant individuals were related to high species richness of forest and shrub-land birds, whereas open-country birds avoided such areas. The species richness and total number of forest birds declined with increasing distance to the forest. A comparison with the bird community within Kakamega Forest indicated that

only a fraction of the forest species could be sustained in the farmland. This suggests that agroecosystems with a diverse habitat structure can support a high diversity of birds, but have only a limited capacity to compensate for forest loss.

Keywords Bird diversity · Africa · Agriculture · Habitat structure · Land-use

Introduction

Ecological research in agroecosystems gains in importance as anthropogenic land-cover change accelerates, especially in the tropics (Vandermeer and Perfecto 1997; Petit et al. 1999). Worldwide, tropical forests are turned into landscapes dominated by human use, mostly land intensively used for agriculture (Greenberg et al. 1997b; Daily et al. 2001). Yet, little is known about the ecology of tropical agroecosystems and the factors that influence their capacity to sustain tropical biodiversity. It is particularly important to determine under which conditions and to what extent agroecosystems can compensate for the destruction and fragmentation of natural habitat. In the tropics, rural areas with high human population density are particularly prone to forest loss (Wright 2005). At the same time, these areas often harbour especially high biodiversity (Balmford et al. 2001). Thus, areas densely settled by man and with high biodiversity are particularly important for further investigations.

Tropical birds are comparatively well known and easy to monitor, and have been successfully used to investigate the influence of land-use change (Kofron and Chapman 1995; Söderström et al. 2003; Waltert et al. 2005). The bird diversity of tropical agroecosystems depends on cultivation

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method, vegetation structure and intensity of land-use (Estrada et al. 1997; Luck and Daily 2003). In Europe, the intensification of agriculture with high-input farming practices has been identified as a major threat to bird diversity (EBCC 2007). In contrast, many tropical agroecosystems are characterised by smallholder farms and a lack of access to capital-intensive technology (Brookfield et al. 2003). The resulting small-scale structures and high agrobiodiversity may provide unique opportunities for bird conservation.

Two particularly important factors that influence avian diversity in agricultural settings are habitat structure and distance to the nearest natural forest. Trees and shrubs have a particularly positive effect on bird diversity, and tree height, tree density, and plant diversity are important factors affecting species richness (MacArthur and MacArthur 1961; Thiollay 1995; Greenberg et al. 1997a; Hughes et al. 2002; Harvey et al. 2006). Finally, some studies found higher bird diversity closer to remaining forest (Estrada et al. 1997; Luck and Daily 2003; Naidoo 2004), whereas others detected no such distance effect (Daily et al. 2001).

The effects of habitat structure and distance to nearest forest are expected to differ for groups of birds with different habitat preferences and for different feeding guilds. For example, forest birds may be found more frequently in areas with high tree cover and in close proximity to remaining forest (Naidoo 2004). Frugivorous birds are of particular interest because they can transport seeds of forest tree species from the forest into agricultural land (Chapman and Chapman 1999; Ortiz-Pulido et al. 2000). Forest regeneration, particularly in degraded, fallow agricultural areas, depends on external seed input, for example through seeds dropped by frugivorous birds (Holl 1998; Martinez-Garza and Gonzalez-Montagut 1999).

We studied the bird community of an agroecosystem near Kakamega Forest, western Kenya. Information on bird communities in Afrotropical agroecosystems is particularly scarce (Bennun 2000; Waltert et al. 2005) and, to our knowledge, only two studies have been conducted in eastern Africa (Plumptre 1997; Naidoo 2004). The agroecosystem surrounding Kakamega Forest harbours a human population density of 600 people/km² (KIFCON 1994) and is one of the most densely populated rural areas of the world (Blackett 1994). With this study, we thus aim to quantify bird diversity in an agroecosystem with a particularly high human population density and to evaluate which habitat variables influence the bird community.

The objective of this study was to determine the influence of habitat structure and distance from forest on the number of species and individuals of birds. We distinguished between forest, shrub-land and open-country species and placed a particular focus on frugivorous birds. For a first assessment of bird diversity in the farmland and

forest, we additionally compared our results with those from a previous survey of bird diversity within Kakamega Forest (Farwig et al. 2006).

Methods

Study area

We conducted the study from September to December 2004 in farmland bordering Kakamega Forest National Reserve in western Kenya (00°08′–00°22′N, 34°46′–34°57′E, altitude 1,500–1,700 m). Kakamega Forest is Kenya's only remaining mid-altitude tropical rainforest and is regarded as the easternmost relict of the Guineo-Congolian rainforests (Kokwaro 1988). Average annual precipitation is 2,007 mm (average from Forest Department records at Isecheno Forest Station from 1982 to 2001) with rainy seasons from March to May and July to October. Average day temperatures vary between 10.6°C (rainy season) and 27.7°C (dry season) (Tsingalia 1990). Kakamega Forest was designated as important bird area and harbours two globally threatened bird species: Turner's Eremomela (*Eremomela turneri*) and Chapin's Flycatcher (*Muscicapa lendu*) (BirdLife International 2006). Another 15 bird species are regionally threatened (e.g. *Glaucidium tephronotum*, *Prodotiscus insignis* and *Phyllastrephus baumanni*) and 46 bird species are probably found nowhere else in Kenya (Bennun and Njoroge 1999). Savalli (1989) found a total of 358 bird species in and around Kakamega forest.

The area around Kakamega Forest is intensively used for agriculture and has an average population density of 600 people/km² (KIFCON 1994). In the study area (Fig. 1), the farmland is structurally highly diverse. Farmers on small subsistence farms grow maize, beans and vegetables and graze cattle and goats next to their homesteads. Sugarcane is the local cash crop and covers larger fields. Patches of fallow land in different successional stages and isolated forest trees, exotic trees and bushes on homesteads, as well as hedgerows as field boundaries, are abundant. Remnant gallery forest is found along rivers.

Study plots

We defined 56 study plots in the farmland north of Kakamega main forest in varying distances to the forest edge between the main forest and the forest fragment Kisere (Fig. 1). Plot size was 35 m × 35 m. For ease of access, the plots were arranged along seven transects. Minimum distance between plots was 130 m. We recorded the geographical coordinates of each study plot's centre using a GPS receiver (Garmin eTrex Summit). Exact distances to the nearest forest edge,

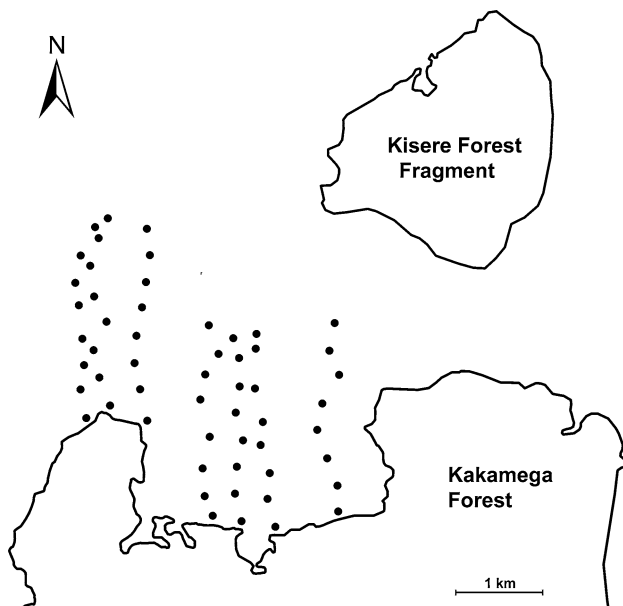


Fig. 1 Position of study plots in the farmland north of Kakamega Forest

being either Kakamega main forest or Kisere, were calculated using a Geographic Information System (ArcGIS 9.1). We also considered distances to the forest fragment Kisere because Kisere is one of the least disturbed forest sites in the general area and harbours a high diversity of primates and birds (Bleher et al. 2006). Seven of the plots were closest to Kisere; the other 49 plots were closest to Kakamega main forest. Distance from forest varied between 71 and 2,141 m.

Bird community

We used point counts to record the birds in each study plot. Standing at the edge, we counted all birds in the study plot for 10 min and identified them to species level using Zimmerman et al. (1999). The plots along one transect were counted during one morning between 0700 and 1000 hours. One bird census, covering all transects in random order, was conducted within 7 days. We repeated the census five times over a total time period of 5 weeks. Repeated counts along the same transect started alternately from south or north. All point counts were carried out in good weather and by the same observers (I. Laube and N. Breitbach).

We divided the birds into groups according to habitat preferences and frugivory. We used the preferred habitats for each species as listed in Zimmerman et al. (1999) to derive a classification into forest species (if listed as preferring forest, forest edge or woodland), shrub-land species (if listed as preferring woodland edge, bush, shrub or

savannah) and open-country species (if listed as preferring grassland, cultivation, marshes or moorland). Bird species were split into frugivorous and non-frugivorous species according to the literature (Urban et al. 1986; Fry et al. 1988; Keith et al. 1992; Urban et al. 1997; Fry et al. 2000; Fry and Keith 2004) and own observations at *Psidium guajava* and *Ficus thonningii* trees in the same area (Eshimwata et al. 2006; Berens et al. 2007).

For statistical analysis, we averaged the number of species and individuals across the five repeated counts per plot to obtain mean numbers per count and plot. Averages were calculated for each bird group separately. Species and individual numbers were $\log(x + 1)$ transformed.

Bird surveys are rarely exhaustive. Often, some species present at a site are not detected. To obtain an estimate of true species richness, we examined first-order jackknife estimates of species richness (150 randomisations), using the software EstimateS (Colwell 2005). This estimator estimates total richness from the observed pattern of relative species abundance across different plots. For the estimation of species richness in the farmland, we converted our bird data to incidences and then pooled the five repeated counts from the same study plot, resulting in a total of 56 sample records, one for each study plot. We calculated species richness estimates for all birds pooled and for forest birds only.

The probability to detect birds during a survey can be influenced by local factors such as the amount of plant cover or the frequency of disturbance. Such variation in detection probabilities can cause variation in the number of observed species, which does not reflect true changes in species richness between sites. To assess such effects for our survey, we calculated detection probabilities after Nichols et al. (1998). To study the detection probability in relation to distance from the forest and number of woody plant individuals, we estimated species richness in different distance classes (distinguishing between point counts <400, 400–699, 700–999, 1,000–1,299, 1,300–1,599, 1,600–1,899 and >1,900 m away from the forest) and different classes of woody cover (distinguishing between point counts with 0–1, 2–6, 7–12, 13–20 and 21–25 woody plants).

We also obtained an estimate of bird species richness inside Kakamega Forest from the data of Farwig et al. (2006), who conducted point counts over plots of the same size (1,225 m²) and over the same time period (10 min). We used bird data from five monthly censuses (September 2001–January 2002) for 54 of their point count locations inside the forest (study plots: Buyangu, Kisere, IsechenoA, IsechenoB, Mukangu, Yala; see Farwig et al. 2006). Our intention in selecting these particular study plots was to use data from near-primary forest in good condition for estimating species richness inside the forest. Again, bird data were converted to incidences and the five counts from the

same locations were pooled, yielding 54 sample records. We then calculated estimates of species richness as described above for all species pooled and for forest species. We also compared total detection probabilities for our farmland survey and the survey inside Kakamega Forest from Farwig et al. (2006).

Habitat structure

To quantify the habitat structure of each study plot, we recorded seven habitat variables: number of woody plant species, number of woody plant individuals, number of habitat types, habitat diversity, length of hedgerows, horizontal vegetation heterogeneity, and vertical vegetation heterogeneity. Number of woody plant individuals was the number of tree and shrub individuals above 2 m height within a plot. Tree and shrub species were identified after Beentje (1994) to obtain number of woody plant species. The number of habitat types within plots was based on the BTO habitat coding scheme classification for farmland (Crick 1992). We did not use categories referring specifically to European crops and created categories suitable for local crops (e.g. sugarcane). An index of habitat diversity was obtained by estimating the percentage cover of the different habitat types to the nearest 5% and calculating the Shannon–Wiener diversity index. We recorded the total length of hedgerows within a plot. Horizontal vegetation heterogeneity was quantified as the coefficient of variation of vegetation height among 20 regularly spaced points within each study plot (Michaels and Cully 1998). Vegetation height of the 20 points was measured using a tape measure or a mirror (James and Shugart 1970). To determine vertical vegetation heterogeneity within each plot, plant cover over the whole study plot was estimated to the nearest 5% at heights of 0, 1, 2, 4, 8 and 16 m. Vertical vegetation heterogeneity was then defined as the diversity of vegetation layers, again using the Shannon–Wiener diversity index (Bibby et al. 2000).

Statistical analysis

To select the variables related to high bird species richness and total abundance, we used a model selection approach based on Akaike's Information Criterion corrected for small sample size (AICc; Burnham and Anderson 2002). This approach has recently received increasing attention as a useful tool for model selection in ecology. The advantage of this approach is that the relative support in the data for competing models can be assessed and parameters can be estimated based on several, equally well supported models (Johnson and Omland 2004).

In our analysis, we followed a two-step process. First, we examined the effect of habitat structure on bird diversity separately and identified the habitat variables with the strongest relation to bird diversity. Second, we analysed the simultaneous effect of the habitat variables selected in the first step and of distance to nearest forest. In this way, we wanted to avoid including habitat variables into our final models that either represented redundant information about the habitat structure or that had only a weak effect on bird diversity.

For the first step, we fitted linear regression models to the data using all possible combinations of the seven habitat variables but retained only models that significantly explained variation in the dataset (log likelihood ratio test, $P \leq 0.05$). We then calculated AICc values of these models. The model with the lowest AICc explains most of the variance with the fewest parameters, i.e. it is the most parsimonious model. It represents a best trade-off between bias, which *decreases* as more parameters are added to the model, and variance, which *increases* with the number of parameters used (Burnham and Anderson 2002). We selected all models whose AICc did not deviate by more than two from the model with the lowest AICc, since models differing by less than two units of AICc can be regarded as equally well supported (Burnham and Anderson 2002). Only habitat variables that were present in these models were used for further analysis.

In the second step, the selected habitat variables and distance to nearest forest were entered together into another model selection process to evaluate their relative importance and simultaneous influence. We used the same model selection procedure as described for the habitat variables above.

For the final best models resulting from this process we calculated Akaike weights to determine how strongly a particular model was supported by the data. Effect strength of the predictor variables was determined using a model averaging approach over the best models to account for possible model selection uncertainty (Johnson and Omland 2004). This was done by multiplying variable coefficients with the model's Akaike weight and summing these products over all models containing the variable of interest. Standard errors and confidence intervals for model averaged coefficients were calculated after Burnham and Anderson (2002). We calculated R^2 values for all models to assess goodness of fit.

This analysis was conducted for number of species and individuals for the following groups of birds, all species pooled, forest species, shrub-land species, open-country species, frugivorous species and frugivorous forest species. The predictor variables number of woody plant individuals, number of habitats, habitat diversity, length of hedges and horizontal vegetation heterogeneity were $\log(x + 1)$

transformed to improve model fit and reduce the influence of outliers. Data analysis was conducted using Statistica 6.0 (2001).

Results

Farmland bird community

During the point counts we observed a total of 1,788 birds belonging to 96 species (Table S1; Supplementary material). Among these were 22 forest species (167 individuals), 58 shrub-land species (1,363 individuals) and 16 open-country species (258 individuals). Forty-five species were frugivorous (1,031 individuals). The frugivorous birds consisted of 16 forest species (151 individuals), 26 shrub-land species (792 individuals) and 3 open-country species (88 individuals). None of the bird species we observed were globally or regionally threatened.

The jackknife estimation procedure calculated an expected number of 128.4 ± 6.7 bird species (mean \pm SD, if not otherwise noted) in the farmland. The estimated richness of forest birds was 28.9 ± 2.5 species. Detection probabilities for the different bird groups were very similar (0.73–0.76) and did not vary systematically when counts were grouped according to distance from forest or number of woody plant individuals. An exception were forest birds, whose detection probability increased slightly with higher number of woody plant individuals (Spearman rank correlation: $\rho = 0.9$, $P = 0.0374$, $n = 5$) (data not shown).

Factors influencing farmland birds

After the first model selection process, we retained between two and six habitat variables depending on the respective bird group (Table S2; Supplementary material). The second model selection process selected between three and six best models (Δ AICc < 2) for the respective bird group (Table 1). Number of woody plant individuals had the strongest positive influence on the number of species and individuals if all bird species were pooled (Table 2). There was no effect of distance to nearest forest for all birds pooled. The number of forest bird species and individuals increased with higher vertical vegetation heterogeneity (Fig. 2a) and decreased slightly, but with high confidence, with increasing distance from the forest (effect size 0.2 species and 0.3 individuals per km; Table 2; Fig. 2b). Shrub-land bird species and individuals increased with increasing number of woody plant individuals and showed no distance effect (Table 2). The number of open-country species was negatively influenced by the number of woody plant individuals whereas open-country individuals

decreased with increasing vertical vegetation heterogeneity (Table 2). We found no distance effect for this group.

The number of frugivorous species and individuals increased with increasing number of woody plant individuals in the plots (Table 2). Frugivorous birds were not influenced by distance from forest. Higher vertical vegetation heterogeneity had a positive influence on the number of species and individuals of frugivorous forest birds (Table 2). Also, frugivorous forest bird species and individuals decreased slightly, but with high confidence, with increasing distance from forest (effect size 0.2 species and 0.3 individuals per km).

Forest bird community

Bird species richness inside Kakamega Forest, as derived from Farwig et al. (2006), was 66 species in total and 54 forest species. Species richness using the jackknife estimation procedure was estimated as 77.8 ± 3.9 species for all species pooled and 62.8 ± 3.6 for forest birds. The detection probability inside Kakamega Forest was slightly higher than in the farmland (0.85 vs 0.75).

Discussion

The number of species and individuals of birds in the farmland near Kakamega Forest was high and was determined mainly by the number of woody plant individuals and vertical vegetation heterogeneity within the study plots. Furthermore, forest birds and frugivorous forest birds declined with increasing distance from the forest.

In general, the farmland around Kakamega Forest supported a highly diverse bird community. Altogether, we detected 96 species. Applying EstimateS on survey data obtained with similar effort inside the forest (Farwig et al. 2006), species richness in the farmland was estimated to be higher than in the forest (128.4 ± 6.7 vs 77.8 ± 3.9 species). Thus, also compared with Kakamega forest, species richness in the farmland near the forest was high. Several studies (Tryjanowski 1999; Kujawa and Tryjanowski 2000; Manning et al. 2006; Harvey et al. 2006) suggest that the occurrence of trees in a variety of spatial configurations and densities may play a particularly important role for sustaining high bird diversity in agroecosystems. In the farmland north of Kakamega Forest, woody cover is very high. In spite of the high human population density and the intensive agricultural use, we recorded a mean number of 14.2 woody plants >2 m height and 13.4 m of hedge per 0.12 ha plot.

The most important factors influencing the farmland bird community in the vicinity of Kakamega Forest were

Table 1 Best models for number of bird species and individuals

Bird category	Species		Individuals		AICc	Δ AICc	w_i	R^2		
	Best models		Best models							
All	1. No. woody plants	39.95	0	0.5	0.1	1. Vertical VH, no. woody plants	84.45	0	0.4	0.1
	2. Vertical VH, no. of woody plants	41.18	0.22	0.5	0.1	2. No. woody plants	84.5	0.05	0.3	0.1
Forest birds						3. No. woody plants, hedges	85.85	1.4	0.2	0.1
						4. Vertical VH, no. woody plants, hedges	86.21	1.77	0.1	0.1
	2. Vertical VH, horizontal VH, distance	0.83	0.54	0.4	0.3	2. Vertical VH, horizontal VH, hedges, distance	89.75	0.49	0.3	0.3
	3. Vertical VH, no. woody plant species, distance	1.81	0.99	0.2	0.3	3. Vertical VH, horizontal VH, distance	50.25	0.5	0.2	0.3
	4. Vertical VH, horizontal VH, hedges, distance	2.62	1.8	0.2	0.3	4. Vertical VH, horizontal VH, no. woody plant species, hedges, distance	51.19	1.44	0.1	0.4
Shrub-land birds	1. No. woody plants	31.24	0	0.3	0.3	5. Vertical VH, hedges, distance	51.6	1.85	0.1	0.3
	2. Horizontal VH, no. woody plants	31.62	0.39	0.2	0.3	1. No. woody plants	68.49	0	0.4	0.3
	3. Woody plant species, no. woody plants	32.61	1.37	0.1	0.3	2. Horizontal VH, no. woody plants	68.75	0.26	0.4	0.3
	4. Horizontal VH, no. woody plant species, no. woody plants	32.9	1.67	0.1	0.3	3. No. woody plant species, no. woody plants	70.37	1.88	0.2	0.3
	5. Vertical VH, no. woody plants	33.17	1.93	0.1	0.3					
	6. Vertical VH, horizontal VH, no. woody plants	33.18	1.95	0.1	0.3					
Open-country birds	1. No. woody plant species, hedges	39.23	0	0.3	0.2	1. Vertical VH	109.1	0	0.4	0.2
	2. Vertical VH, no. woody plant species, hedges	39.44	0.21	0.3	0.3	2. Vertical VH, hedges	110	0.87	0.3	0.2
	3. Vertical VH, no. woody plant species	39.88	0.65	0.2	0.2	3. Vertical VH, no. woody plant species, hedges	110.7	1.67	0.2	0.2
Frugivorous birds	4. No. woody plant species	40.58	1.35	0.2	0.2	4. Vertical VH, no. woody plant species	110.9	1.83	0.2	0.2
	1. No. woody plants	49.81	0	0.3	0.2	1. No. woody plants	88.38	0	0.3	0.2
	2. Horizontal VH, no. woody plants	51.09	1.28	0.2	0.2	2. Horizontal VH, no. woody plants	89.46	1.08	0.2	0.2
	3. No. woody plants, hedges	51.34	1.52	0.2	0.2	3. No. habitats, no. woody plants	89.81	1.43	0.2	0.2
	4. Habitat diversity, no. woody plants	51.4	1.58	0.1	0.2	4. No. woody plants, hedges	89.85	1.47	0.1	0.2
	5. No. habitats, no. woody plants	51.73	1.91	0.1	0.2	5. No. habitats, no. woody plants	90.03	1.65	0.1	0.2
6. No. woody plant species, no. woody plants	51.8	1.99	0.1	0.2	6. Vertical VH, no. woody plants,	90.35	1.97	0.1	0.2	

Table 1 continued

Bird category	Species				Individuals					
	Best models	AICc	Δ AICc	w_i	R^2	Best models	AICc	Δ AICc	w_i	R^2
Frugivorous forest birds	1. Vertical VH, horizontal VH, distance	-3.92	0	0.2	0.3	1. Vertical VH, horizontal VH, distance	48.16	0	0.3	0.4
	2. Vertical VH, distance	-3.41	0.51	0.2	0.3	2. Horizontal VH, distance	48.47	0.3	0.3	0.3
	3. No. woody plants, distance	-2.94	0.99	0.1	0.2	3. Distance	49.07	0.91	0.2	0.3
	4. Vertical VH, no. woody plants, distance	-2.55	1.37	0.1	0.3	4. Horizontal VH, no. woody plant species, hedges, distance	49.53	1.36	0.2	0.4
	5. Vertical VH, horizontal VH, hedges, distance	-2.48	1.45	0.1	0.3					
	6. Vertical VH, no. woody plant species, distance	-2.08	1.85	0.1	0.3					
	7. Vertical VH, horizontal VH, habitat diversity, distance	-2.07	1.86	0.1	0.3					
	8. No. woody plant species, distance	-1.99	1.94	0.1	0.2					

All variables except no. woody plant species and vertical vegetation heterogeneity were $\log(x + 1)$ transformed

AICc Akaike's information criterion corrected for small sample size, Δ AICc difference in AICc to best model, w_i Akaike weight, R^2 coefficient of determination, no. woody plants number of woody plant individuals, *habitat diversity* Shannon–Wiener index of habitat types, *hedges* length of hedgerows, *horizontal VH* horizontal vegetation heterogeneity, *vertical VH* vertical vegetation heterogeneity, *distance* distance from forest

vertical vegetation heterogeneity and number of woody plant individuals. The prevalent importance of these factors agrees with other studies of bird communities in tropical agroecosystems (Greenberg et al. 1997a; Petit et al. 1999; Hughes et al. 2002; Söderström et al. 2003; Waltert et al. 2005). Detection probabilities did not vary with bird group or number of woody plant individuals, so our observed community composition was a good representation of the true bird community.

Species richness of forest birds was highest in areas with high vertical vegetation heterogeneity. Such patterns have been found in tropical as well as temperate locations (e.g. MacArthur and MacArthur 1961; Greenberg et al. 1997a; Hughes et al. 2002). The negative effect of distance from forest on forest birds was weak, but statistically very well confirmed. Forest bird detection probabilities did not change with increasing distance from forest, further strengthening the evidence for a true distance effect. The small effect size of the distance effect might be related to the high habitat complexity of the farmland which may allow relatively unrestrained movement of forest birds across the spatial scale we investigated (71–2,141 m). Other studies also find a decline of forest birds with distance from forest (Estrada et al. 1997; Luck and Daily 2003). Naidoo (2004) reports a slightly higher decline of one forest species per km for the area around Mabira Forest Reserve in Uganda, where smallholder agriculture is characterised by lower numbers of trees. The majority of the forest birds we observed in the farmland are known to have rather flexible habitat requirements. Forest specialists as classified by Bennun et al. (1996) accounted for only 4 of the 22 forest species (18.2%; *Nectarinia olivacea*, *Phylloscopus budongoensis*, *Ploceus insignis*, *Serinus burtoni tanganjicae*) and 11 of the 167 forest individuals (6.6%) in the farmland. The birds seen by us in the farmland were mainly foraging. We made no observations suggesting that forest birds nested in the farmland. Equally, observations of birds clearly on transit were very rare. Studies of frugivore communities at trees in the farmland around Kakamega Forest also report foraging forest birds (Eshiamwata et al. 2006; Berens et al. 2007). Thus, it seems that some forest species can use the heterogeneous farmland close to Kakamega Forest to gain access to additional food resources.

Shrub-land birds were mainly influenced by the number of woody plant individuals (see also Söderström et al. 2003), whereas they showed no clear relationship with vertical vegetation heterogeneity. This might indicate a reduced importance of vegetation structure below 2 m height for this group or less specialised demands for diversity in tree cover compared to forest birds. Shrub-land birds are the most numerous birds in our study, both in terms of species and individuals. Thus, the patterns for all

Table 2 Model averaging

Bird category	Variable	Species			Individuals		
		Estimate	SE	95% CI	Estimate	SE	95% CI
All	No. woody plants	0.10	0.04	0.02	0.18	0.07	0.29
	Hedges	–	–	–	–	0.02	0.04
Forest birds	Vertical VH	–0.07	0.07	–0.21	0.08	0.12	0.09
	No. woody plant species	0.002	0.003	–0.003	0.01	0.003	0.01
Shrub-land birds	Hedges	–0.003	0.004	–0.01	0.004	0.02	0.01
	Horizontal VH	0.11	0.09	–0.07	0.30	0.18	0.63
Open-country birds	Vertical VH	0.20	0.09	0.03	0.36	0.13	0.58
	Distance	-2.00×10^{-4}	5.00×10^{-5}	-3.00×10^{-4}	-1.00×10^{-4}	1.00×10^{-4}	-1.00×10^{-4}
Frugivorous birds	No. woody plants	0.19	0.05	0.10	0.29	0.06	0.39
	No. woody plant species	–0.005	0.006	–0.02	0.01	0.005	0.01
Frigivorous forest birds	Horizontal VH	–0.14	0.12	–0.37	0.10	0.15	0.13
	Vertical VH	–0.02	0.03	–0.08	0.04	–	–
Open-country birds	No. woody plant species	–0.04	0.01	–0.07	–0.01	0.01	0.01
	Hedges	0.03	0.02	–0.01	0.07	0.03	0.09
Frugivorous birds	Vertical VH	–0.11	0.09	–0.28	0.06	0.24	–0.20
	No. woody plants	0.14	0.05	0.05	0.24	0.06	0.34
Frigivorous forest birds	No. woody plant species	–0.001	0.003	–0.01	0.004	–	–
	No. habitats	–0.01	0.02	–0.06	0.03	0.04	0.05
Open-country birds	Habitat diversity	–0.02	0.03	–0.08	0.04	0.05	0.06
	Hedges	–0.004	0.006	–0.02	0.01	0.01	0.01
Frugivorous forest birds	Horizontal VH	–0.04	0.05	–0.14	0.06	0.08	0.09
	Vertical VH	–	–	–	–	0.03	0.06
Open-country birds	No. woody plants	0.01	0.01	–0.01	0.03	–	–
	No. woody plant species	0.002	0.002	–0.002	0.01	0.003	0.01
Frugivorous forest birds	Habitat diversity	–0.01	0.01	–0.03	0.02	–	–
	Hedges	–0.002	0.003	–0.01	0.003	0.02	0.01
Open-country birds	Horizontal VH	0.10	0.08	–0.06	0.26	0.19	0.73
	Vertical VH	0.13	0.07	–0.01	0.27	0.13	0.56
Frugivorous forest birds	Distance	-2.00×10^{-4}	5.00×10^{-5}	-3.00×10^{-4}	-1.00×10^{-4}	1.00×10^{-4}	-1.00×10^{-4}

Influence of variables in best models on number of bird species and individuals. Confidence intervals not containing zero are printed in bold. All variables except no. woody plant species and vertical vegetation heterogeneity were $\log(x + 1)$ transformed

Estimate model averaged beta coefficient, SE model averaged standard error, 95% CI 95% confidence interval, no. woody plants number of woody plant individuals, habitat diversity Shannon–Wiener index of habitat types, hedges length of hedge rows, horizontal VH horizontal vegetation heterogeneity, vertical VH vertical vegetation heterogeneity, distance distance from forest

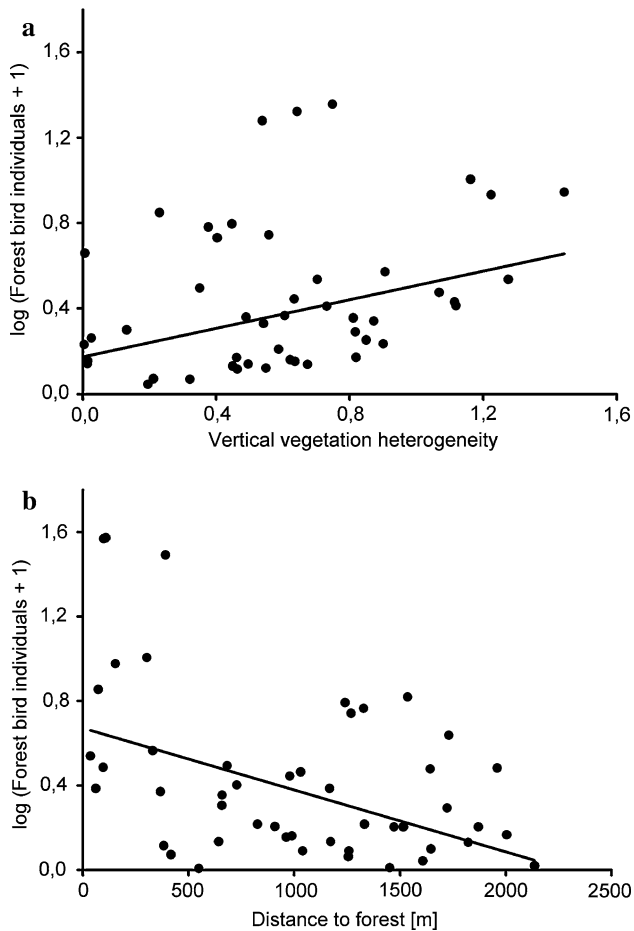


Fig. 2 **a** Effect of vertical vegetation heterogeneity on forest bird abundance if distance from forest was controlled for. **b** Effect of distance from forest on forest bird abundance if vertical vegetation heterogeneity was controlled for. The plots are based on a model with distance to forest and vertical vegetation heterogeneity as predictors, which was among the best models for forest bird abundance (Table 1). Shown are JMP partial leverage plots

bird species pooled were similar to those of shrub-land species. Open-country birds avoided habitat with high vertical vegetation heterogeneity or many woody plant species. This is consistent with our expectations based on the habitat description for this bird group in the literature.

Frugivorous bird numbers depended mainly on the number of woody plant individuals in the plots. Frugivorous forest birds increased with vertical vegetation heterogeneity and declined slightly with distance to the nearest forest. Bird mobility between forest and farmland has important consequences for forest regeneration on fallow land through seed dispersal (Martinez-Garza and Gonzalez-Montagut 1999; Chapman and Chapman 1999; Holl et al. 2000). High vertical vegetation cover in the farmland might stimulate forest birds to visit the farmland more often. At the same time, such farmland areas can sustain a high diversity of shrub-land birds occasionally

visiting the forest. Fifty-three percent of our shrub-land birds were classified as forest visitors or forest generalists by Bennun et al. (1996) and ten shrub-land species were observed visiting Kakamega Forest in the subset of data we used from Farwig et al. (2006). Thus, high vertical vegetation heterogeneity and many woody plants might also increase bird mobility between farmland and forest and may result in higher seed rain of forest tree species on agricultural land.

The comparison of forest-dependent birds between farmland and forest demonstrates that most forest species were probably restricted to Kakamega Forest. The species richness estimate of forest birds in the farmland was much lower than the one found for forest birds inside Kakamega forest (28.9 ± 6.5 vs 62.8 ± 3.6 species). Detection probabilities for forest and farmland indicate that this comparison is valid and not influenced by birds being more difficult to locate in dense forest. Altogether, 194 forest-dependent species are cited for Kakamega forest (Bennun and Njoroge 1999), of which we documented only 11% in the farmland. Waltert et al. (2005) also observed a marked change in bird community composition from intact forest to annual cultures near Korup National Park in Cameroon. Other studies from Costa Rica (Daily et al. 2001), Liberia (Kofron and Chapman 1995), Ivory Coast (Waltert 2000) and Nigeria (Elgood and Sibley 1964) suggest a regional species loss of 66–71% if tropical forests were converted to agroecosystems. Moreover, the mere presence of a forest bird in the farmland is no indication that this species is able to maintain an independent population in the farmland and is not dependent on nearby forest habitat. Overall, our results suggests that the conservation of the native forest bird fauna in the agroecosystem near Kakamega Forest appears possible for only a very limited number of species (see also Thiollay 1995; Naidoo 2004; Tejada-Cruz and Sutherland 2004).

To conclude, the farmland near Kakamega Forest exhibits, despite high human population densities and intensive agricultural use, a high structural habitat diversity, which in turn supports high bird diversity. High vertical vegetation heterogeneity and many woody plants were related to high species richness of forest and shrub-land species. Both habitat variables can be recorded in the field with little effort. Thus, vertical vegetation heterogeneity and number of woody plant individuals appear to be useful indicators for high bird diversity in agricultural landscapes in Kenya and perhaps generally in the tropics. Moreover, structurally complex farmland appeared to have enhanced the mobility of frugivorous birds between forest and farmland, potentially increasing seed rain of forest trees on agricultural areas and forest regeneration. Thus, tropical agroecosystems do have the potential to sustain both a high rural human population density and a high bird

diversity (Daily et al. 2001). Some studies even suggest that, in the Kenyan highlands, a rising population size was accompanied by agricultural changes beneficial to bird diversity in the farmland (Tiffen et al. 1994). Agricultural intensification around Kakamega Forest is accompanied with practices such as crop diversification, intercropping and cover crops, an increase in agroforestry, and the reduction of communal grazing lands, which in turn meant less soil erosion and more vegetation cover (Bradley 1988; Connelly and Chaiken 2000). However, species richness and total abundance of forest birds declined with increasing distance from the forest and only a few forest bird species were found outside the forest indicating that even this highly diverse agroecosystem cannot compensate for the loss of tropical forests.

Zusammenfassung

Vogeldiversität in einem kenianischen Agro-Ökosystem: Einfluss von Habitatstruktur und Entfernung zum Wald

Tropische Agrar-Ökosysteme bedecken zunehmend größere Teile der Landmasse unserer Erde. Trotzdem ist wenig über die Faktoren bekannt, welche die Avifauna beeinflussen. Dies gilt umso mehr für Gebiete mit hoher Bevölkerungsdichte. Das Potential tropischen Farmlandes für den Erhalt von Vogelbiodiversität, speziell die der Waldvögel, kann von der Habitatstruktur und der Distanz zum nächstgelegenen Wald beeinflusst werden. Wir untersuchten den Einfluss dieser beiden Faktoren auf die Vogelgemeinschaft nahe des Kakamega Forest in Kenia. Mit Hilfe von Punkt-Stopp-Zählungen ermittelten wir die Anzahl der Vogelarten und -individuen auf 56 bis zu 2.100 m vom Wald entfernten Untersuchungsflächen. Wir beobachteten dabei insgesamt 96 Vogelarten im Agrarland. Davon waren 22 Waldarten, 58 Buschlandarten und 16 Offenlandarten. Eine hohe vertikale Vegetationsheterogenität und eine hohe Individuenzahl holziger Pflanzen standen mit einer hohen Artenzahl an Wald- und Buschlandarten in Beziehung, während Offenlandarten solche Gebiete mieden. Die Artenzahl und die Gesamtanzahl an Waldvogelarten nahmen mit zunehmender Entfernung zum Wald hin ab. Ein Vergleich der Vogelgemeinschaft innerhalb des Kakamega Forest deutete darauf hin, dass lediglich ein Teil der Waldvogelarten im umliegenden Agrarland erhalten werden könnte. Dies legt nahe, dass Agrar-Ökosysteme zwar mit diversen Habitatstrukturen eine hohe Diversität an Vögeln beherbergen können. Jedoch vermögen sie nur in begrenztem Maße, den Verlust von Wald zu kompensieren.

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References

- Balmford A, Moore JL, Brooks T, Burgess N, Hansen LA, Williams P, Rahbek C (2001) Conservation conflicts across Africa. *Science* 291:2616–2619 doi:10.1126/science.291.5513.2616
- Beentje H (1994) Kenya trees, shrubs and lianas. National Museums of Kenya, Nairobi
- Bennun LC (2000) Assessing and monitoring bird populations in Africa: an overview. *Ostrich* 71:214–215
- Bennun L, Njoroge P (1999) Important bird areas in Kenya. Nature Kenya, Nairobi
- Bennun LC, Dranzoa C, Pomeroy D (1996) The forest birds of Kenya and Uganda. *J East Afr Nat Hist* 85:23–48
- Berens DG, Farwig N, Schaab G, Böhning-Gaese K (2007) Exotic guavas are foci of forest regeneration in kenyan farmland. *Biotropica*. doi:10.1111/j.1744-7429.2007.00338.x
- Bibby CJ, Burgess ND, Hill DA, Mustoe SH (2000) Bird census techniques. Academic, London
- BirdLife International (2006) Species factsheets. Available online at <http://www.birdlife.org>
- Blackett HL (1994) Forest inventory report no. 3 Kakamega. Forest Dept./KIFCON, Nairobi
- Bleher B, Uster D, Bergsdorf T (2006) Assessment of threat status and management effectiveness in Kakamega Forest, Kenya. *Biodivers Conserv* 15:1159–1177 doi:10.1007/s10531-004-3509-3
- Bradley PN (1988) Methodology for woodland development planning in the Kenyan highlands. *J Biogeogr* 15:157–164
- Brookfield H, Parsons H, Brookfield M (eds) (2003) Agrodiversity: learning from farmers across the world. United Nations University Press, Tokyo
- Burnham KP, Anderson DR (2002) Model selection and multi-model inference, 2nd edn. Springer, New York Berlin Heidelberg
- Chapman CA, Chapman J (1999) Forest restoration in abandoned agricultural land: a case study from East Africa. *Conserv Biol* 13:1301–1311 doi:10.1046/j.1523-1739.1999.98229.x
- Crick HQP (1992) A bird-habitat coding system for use in Britain and Ireland incorporating aspects of land management and human activity. *Bird Study* 39:1–12
- Colwell RK (2005) EstimateS: statistical estimation of species richness and shared species from samples. Version 7.5. Available online at <http://purl.oclc.org/estimates>
- Connelly WT, Chaiken MS (2000) Intensive farming, agro-diversity, and food security under conditions of extreme population pressure in western Kenya. *Hum Ecol* 28:19–51
- Daily GC, Ehrlich PR, Sanchez-Azofeifa GA (2001) Countryside biogeography: use of human-dominated habitats by the avifauna of southern Costa Rica. *Ecol Appl* 11:1–13
- EBCC (2007) Trends of common birds in Europe, 2007 update. Available online at <http://www.ebcc.info/pecbm.html>
- Elgood JH, Sibley FC (1964) The tropical forest edge avifauna of Ibadan, Nigeria. *Ibis* 106:221–248
- Eshiamwata GW, Berens DG, Bleher B, Dean WRJ, Böhning-Gaese K (2006) Bird assemblages in isolated *Ficus* trees in Kenyan farmland. *J Trop Ecol* 22:723–726

- Estrada A, Coates-Estrada R, Merritt DA (1997) Anthropogenic landscape change and avian diversity at Los Tuxtlas, Mexico. *Biodivers Conserv* 6:19–43 doi:[10.1023/A:1018328930981](https://doi.org/10.1023/A:1018328930981)
- Farwig N, Böhning-Gaese K, Bleher B (2006) Enhanced seed dispersal of *Prunus africana* in fragmented and disturbed forests? *Oecologia* 47:238–252. doi:[10.1007/s00442-005-0288-9](https://doi.org/10.1007/s00442-005-0288-9)
- Fry CH, Keith S (eds) (2004) *The birds of Africa*, vol VII. Christopher Helm, London
- Fry CH, Keith S, Urban KE (eds) (1988) *The birds of Africa*, vol III. Academic, London
- Fry CH, Keith S, Urban KE (eds) (2000) *The birds of Africa*, vol VI. Academic, London
- Greenberg R, Bichier P, Angon AC, Reitsma R (1997a) Bird populations in shade and sun coffee plantations in central Guatemala. *Conserv Biol* 11:448–459 doi:[10.1046/j.1523-1739.1997.95464.x](https://doi.org/10.1046/j.1523-1739.1997.95464.x)
- Greenberg R, Bichier P, Sterling J (1997b) Bird populations in rustic and planted shade coffee plantations of eastern Chiapas, Mexico. *Biotropica* 29:501–514 doi:[10.1111/j.1744-7429.1997.tb00044.x](https://doi.org/10.1111/j.1744-7429.1997.tb00044.x)
- Harvey CA, Medina A, Sánchez DM, Vélchez S, Hernández B, Saenz JC, Maes JM, Casanoves F, Sinclair FL (2006) Patterns of animal diversity in different forms of tree cover in agricultural landscapes. *Ecol Appl* 16:1986–1999
- Holl KD (1998) Do bird perching structures elevate seed rain and seedling establishment in abandoned tropical pastures? *Restor Ecol* 6:253–261 doi:[10.1046/j.1526-100X.1998.00638.x](https://doi.org/10.1046/j.1526-100X.1998.00638.x)
- Holl KD, Loik ME, Lin EH, Samuels IA (2000) Tropical montane forest restoration in Costa Rica: overcoming barriers to dispersal and establishment. *Restor Ecol* 8:339–349 doi:[10.1046/j.1526-100x.2000.80049.x](https://doi.org/10.1046/j.1526-100x.2000.80049.x)
- Hughes JB, Daily GC, Ehrlich PR (2002) Conservation of tropical forest birds in countryside habitats. *Ecol Lett* 5:121–129 doi:[10.1046/j.1461-0248.2002.00294.x](https://doi.org/10.1046/j.1461-0248.2002.00294.x)
- James FC, Shugart HH (1970) A quantitative method of habitat description. *Audubon Field Notes* 24:727–736
- Johnson JB, Omland KS (2004) Model selection in ecology and evolution. *Trends Ecol Evol* 19:101–108
- Keith S, Urban KE, Fry CH (eds) (1992) *The birds of Africa*, vol IV. Academic, London
- KIFCON (1994) *Kakamega guide. The official guide. Kenya Indigenous Forest Conservation Programme*, Nairobi
- Kofron CP, Chapman A, (1995) Deforestation and bird species composition in Liberia, West Africa. *Trop Zool* 8:239–256
- Kokwaro JO (1988) Conservation status of the Kakamega Forest in Kenya. The Eastern most relic of the equatorial rainforest of Africa. *Monogr Syst Bot Mo Bot Gard* 25:471–489
- Kujawa K, Tryjanowski P (2000) Relationships between the abundance of breeding birds in Western Poland and the structure of agricultural landscape. *Acta Zool Acad Sci Hung* 46:103–114
- Luck GW, Daily GC (2003) Tropical countryside bird assemblages: richness, composition and foraging differ by landscape context. *Ecol Appl* 13:235–247
- MacArthur RH, MacArthur JW (1961) On bird species diversity. *Ecology* 42:594–598
- Manning AD, Fischer J, Lindenmayer DB (2006) Scattered trees are keystone structures—implications for conservation. *Biol Conserv* 132:311–321
- Martinez-Garza C, Gonzalez-Montagut R (1999) Seed rain from forest fragments into tropical pastures in Los Tuxtlas, Mexico. *Plant Ecol* 145:255–265 doi:[10.1023/A:1009879505765](https://doi.org/10.1023/A:1009879505765)
- Michaels HL, Cully JF (1998) Landscape and fine scale habitat associations of the Loggerhead shrike. *Wilson Bull* 110:474–482
- Naidoo R (2004) Species richness and community composition of songbirds in a tropical forest-agricultural landscape. *Anim Conserv* 7:93–105 doi:[10.1017/S1367943003001185](https://doi.org/10.1017/S1367943003001185)
- Nichols JD, Bouligner T, Hines JE, Pollock KH, Sauer JR (1998) Inference methods for spatial variation and community composition when not all species are detected. *Conserv Biol* 12:1390–1398 doi:[10.1046/j.1523-1739.1998.97331.x](https://doi.org/10.1046/j.1523-1739.1998.97331.x)
- Ortiz-Pulido R, Laborde J, Guevara S (2000) Fruit-eating habits of birds in a fragmented landscape: Implications for seed dispersal. *Biotropica* 32:473–488 doi:[10.1111/j.1744-7429.2000.tb00494.x](https://doi.org/10.1111/j.1744-7429.2000.tb00494.x)
- Petit LJ, Petit DR, Christian DG, Powell HD (1999) Bird communities of natural and modified habitats in Panama. *Ecography* 22:292–304 doi:[10.1111/j.1600-0587.1999.tb00505.x](https://doi.org/10.1111/j.1600-0587.1999.tb00505.x)
- Plumptre AJ (1997) Shifting cultivation along the trans-African highway and its impact on the understorey bird community in the Ituri Forest, Zaire. *Bird Conserv Int* 7:317–329
- Savalli UM (1989) Checklist of bird of the Kakamega Forest and National Reserve. Available online at <http://www.uky.edu/~cfox/Students/Savalli/KakaBirdList.html>
- Söderström B, Kiema S, Reid RS (2003) Intensified agricultural land-use and bird conservation in Burkina Faso. *Agric Ecosyst Environ* 99:113–124 doi:[10.1016/S0167-8809\(03\)00144-0](https://doi.org/10.1016/S0167-8809(03)00144-0)
- Tejeda-Cruz C, Sutherland WJ (2004) Bird responses to shade coffee production. *Anim Conserv* 7:169–179 doi:[10.1017/S1367943004001258](https://doi.org/10.1017/S1367943004001258)
- Thiollay JM (1995) The role of traditional agroforests in the conservation of rain-forest bird diversity in Sumatra. *Conserv Biol* 9:335–353 doi:[10.1046/j.1523-1739.1995.9020335.x](https://doi.org/10.1046/j.1523-1739.1995.9020335.x)
- Tiffen M, Mortimore M, Gichuki F (1994) *More people, less erosion. Environmental recovery in Kenya*. Wiley, Chichester
- Tryjanowski P (1999) Effect of habitat diversity on breeding birds: comparison of farmland bird community in the region of Wielkopolska (W. Poland) with relevant data from other European studies. *Pol J Ecol* 47:153–174
- Tsingalia MH (1990) Habitat disturbance, severity and patterns of abundance in Kakamega Forest, Western Kenya. *Afr J Ecol* 28:213–226
- Urban EK, Fry CH, Keith S (eds) (1986) *The birds of Africa*, vol II. Academic, London
- Urban EK, Fry CH, Keith S (eds) (1997) *The birds of Africa*, vol V. Academic, London
- Vandermeer J, Perfecto I (1997) The agroecosystem: a need for the conservation biologist's lens. *Conserv Biol* 11:591–592 doi:[10.1046/j.1523-1739.1997.07043.x](https://doi.org/10.1046/j.1523-1739.1997.07043.x)
- Waltert M (2000) Diversity and structure of a bird community in a logged forest in south-east Cote d'Ivoire. PhD thesis, University of Göttingen, Germany
- Waltert M, Bobo SK, Saing NM, Fermon H, Mühlenberg M (2005) From forest to farmland: habitat effects on Afrotropical forest bird diversity. *Ecol Appl* 15:1351–1366
- Wright SJ (2005) Tropical forests in a changing environment. *Trends Ecol Evol* 20:553–560 doi:[10.1016/j.tree.2005.07.009](https://doi.org/10.1016/j.tree.2005.07.009)
- Zimmerman DA, Turner DA, Pearson DJ (1999) *Birds of Kenya and northern Tanzania. Field guide edition*. Princeton University Press, New Jersey